PALORCHESTES AZAEL (MAMMALIA, PALORCHESTIDAE) FROM THE LATE PLEISTOCENE TERRACE SITE LOCAL FAUNA, RIVERSLEIGH, NORTHWESTERN QUEENSLAND

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A maxilla of *Palorchestes azael* is described from gravel deposits at Terrace Site, Riversleigh Station. A radiocarbon date of 23,900 +4100 -2700 years BP is reported from the fossiliferous unit at Terrace Site supporting previous interpretations of a late Pleistocene age for the Terrace Site Local Fauna.

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Terrace Site occurs in unconsolidated fluviatile sediments on the eastern bank of the Gregory River 5 km downstream from the Lawn Hill road crossing on Riversleigh Station, NW Queensland. These deposits were interpreted as Pleistocene gravels resting on Tertiary and Cambrian limestones (Archer et al., 1989, 1994). The Terrace Site Local Fauna is listed in Archer et al. (1994).

Material is deposited in the Australian Museum (AMF), the Natural History Museum, London (BM), Museum of Victoria (NMVP), Queensland Museum (QMF), South Australian Museum (SAM), Department of Geology, James Cook University (P). Molar number follows Luckett (1993); premolar number follows Flower (1867); molar crown morphology follows Archer (1984).

STRATIGRAPHY AND AGE

Terrace Site has a 3m high cross-section through horizontal and lenticular beds in an upwardly fining sequence. The basal sediments are poorly sorted, light grey sands and gravels with abundant mussel shell fragments and most of the vertebrates including QMF30882. The section grades upwards into finer sands, silts and clays with finer shell fragments. Charcoal particles up to 5mm occur throughout in small lenses or isolated fragments. The charcoal occurring in lenses, maxilla and most other specimens being unabraded and the recovery of articulated material, suggests that at least part of the fauna and associated charcoal is a primary accumulation.

Based on the mammal fauna the age was interpreted as possibly late Pleistocene (Archer et al.,1994). Charcoal from the basal bone-rich layer that contained QMF30882 gave a conventional radiocarbon date of 23,900 +4100 -2700 BP (ANU-7620). Although the standard errors are high, the range within two standard errors confirms the Late Pleistocene age.

SYSTEMATICS

Order DIPROTODONTIA Owen, 1866
Suborder VOMBATIFORMES Woodburne, 1984
Family PALORCHESTIDAE Tate, 1948 sens. Archer & Bartholomai, 1978

Palorchestes Owen, 1873

TYPE SPECIES *Palorchestes azael* Owen, 1873.

Palorchestes azael Owen, 1873
(Fig. 1; Table 1)

MATERIAL. QMF30882, a left maxillary fragment with near complete M^{1-3}, the fragmented alveolus of P3, and a portion of the palate and jugal.

DESCRIPTION. Upper molars high-crowned, bilophodont, trapezoidal in occlusal view, with the protoloph wider than the metaloph. Lophs broad at their bases, narrow toward the apices, slightly crescentic. Broad anterior and posterior cingula on each tooth, extending around the tooth forming narrow lingual and buccal cingula. Molar enamel crenulated and rough on anterior, posterior and inter-loph surfaces, but smooth on lateral surfaces.

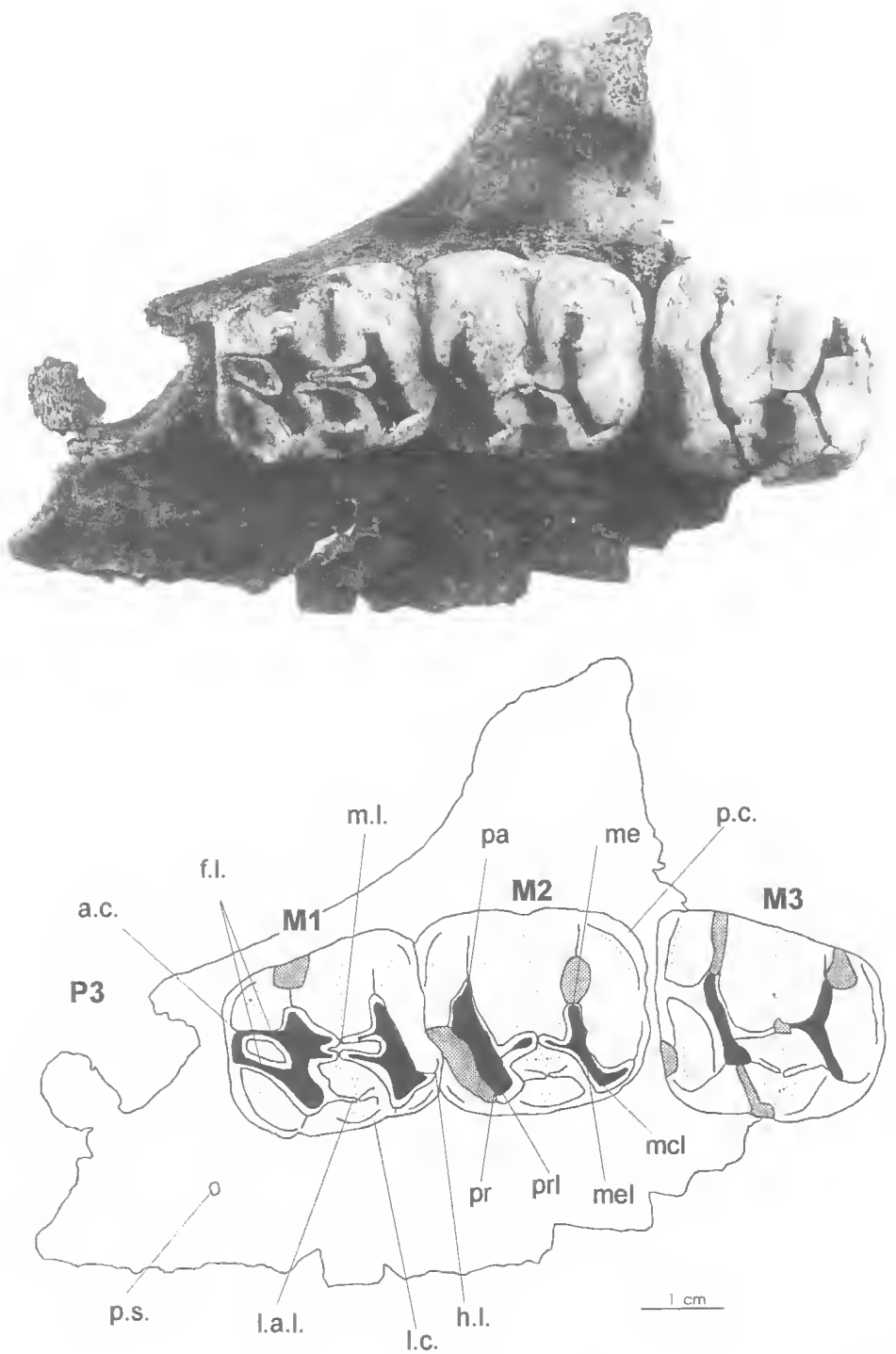


FIG. 1. *Palorchestes azael* Owen, 1873, QMF30882 from Terrace Site, maxillary fragment with M^1-M^3, in occlusal view. a.c.=anterior cingulum; p.c.=posterior cingulum; l.c.=lingual cingulum; f.l.=forelink; m.l.=midlink; h.l.=hindlink; l.a.l.=lingual accessory link; pr=protocone; pa=paracone; me=metacone; mcl=metaconule; prl=protoloph; mel=metaloph; p.s.=palatal sinus.

Table 1. Dimensions (mm) of upper cheek teeth of QMF30882 and comparative samples of *P. azael* (BM46316, AMF452, P186593, AMF7272, QMF7074, QMF772), *P. parvus* (from Woods 1958), *P. painei* (from Woodburne, 1967) and *P. selestiae* (from Mackness, 1995). The dimensions of the holotype of *P. azael* equal the minimum values of the observed ranges.e = estimate; H=holotype.

		QMF 30882	*P. azael*			*P. parvus*			*P. painei*			*P. selestiae* (H)
			N	MEAN	RANGE	N	MEAN	RANGE	N	MEAN	RANGE	
P^3	L	17.0e	2	20.8	18.7-23.7	1	16.8	-	4	13.9	13.8-14.4	-
M^1	L	28.8	6	26.3	23.5-28.7	4	19.6	17.8-22.1	4	17.4	16.5-18.2	22.6
	AW	24.1e	6	23.0	19.3-27.7	4	15.5	14.2-17.3	4	14.2	13.6-14.4	16.6
	PW	23.5	6	21.9	17.1-23.0	3	-	-	3	13.5	13.2-13.8	16.9
M^2	L	29.2e	5	27.2	24.9-29.2	3	20.1	18.7-20.6	3	18.1	17.8-18.1	-
	AW	27.2	5	24.5	21.5-26.8	2	16.3	15.0-17.5	2	15.4	14.8-15.5	-
	PW	24.7	5	22.3	19.9-24.7	3	-	-	3	13.6	13.1-14.3	-
M^3	L	31.5	4	27.4	25.3-31.5	4	21.0	19.6-22.3	4	18.5	18.0-19.4	-
	AW	26.2	3	22.6	19.7-26.0	3	16.6	15.9-17.5	3	15.3	15.0-16.3	-
	PW	24.7	3	20.5	18.1-23.1	4	-	-	4	13.3	12.6-14.1	-
M^1-M^3	L	85.2	3	79.5	74.0-86.4	-	-	-	-	-	-	-

P^3 missing. Partly preserved alveolus suggesting P^3 as subtriangular, about 17 mm long.

M^1 nearly complete, missing only a small part of the enamel of the buccal side of the protoloph, with 2 high forelinks joining the protoloph to a broad anterior cingulum. Lingual forelink offset diagonally, joining the anterior cingulum from the protocone at the midline of the tooth. Deep pits between, and on both sides of, the forelinks. A high double-midlink between the lophs. On the lingual side of the double-midlink is an accessory link forming a deep lingual pit. Lingual accessory link high and well-developed on M^1. Posterior cingulum compressed by molar crowding from M^2; an irregular folded posterior face of the metaloph formed from a thickened crest (hindlink) descending posteriorly from the metaconule.

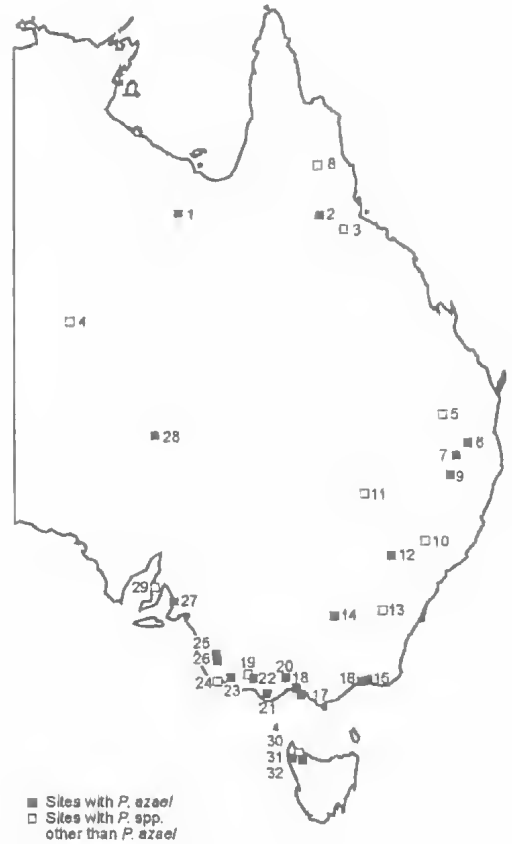
M^2 larger than M^1, missing the anterolingual face of the protoloph, with a single weak forelink, and midlink a single (cf. double in M^1) high link following the midline of the tooth. Lingual accessory link V-shaped in lateral view, differing from the straighter link of M^1 and slightly lower. Anterior and posterior cingula well-developed; anterior cingulum pressed into M^1 because of molar crowding. Hindlink present.

M^3 similar in size and morphology to M^2, differences in length being attributed to molar crowding. Forelink, midlink and hindlink all single. Lingual accessory midlink more reduced than in M^2.

Base of the jugal projecting perpendicular to the maxilla, its anterior edge originating at the M^1-M^2 contact before sloping gradually posteriorly, with its posterior edge perpendicular to the maxilla at the M^2-M^3 junction. A few fragments of the orbital surface preserved on the upper part of the specimen. A minute palatal sinus level with the posterior edge of P^3 alveolus 12 mm from the lingual edge of the tooth row. Only the left side of the palate preserved, extending from the tooth row to near the midpalatal suture.

COMPARISON. QMF30882 compares well with Woods (1958) diagnosis for *P. azael* and its molar dimensions (Table 1) lie within the ranges for *P. azael* and outside those of other species of *Palorchestes*. When compared with a cast of the holotype (BM46316) and description by Owen (1873, pl. 82 fig. 1), the Riversleigh specimen is larger in all dimensions but is otherwise similar. The holotype is the smallest of the comparative sample of *P. azael* examined.

QMF30882 is most similar to AMF452, from Wellington Caves (Dun, 1893, pl. 16), in which the only notable difference is the lingual accessory midlink being only slightly developed in M^1, less so in M^2 and absent in M^3. QMF30882 shows a similar gradient of development from well-developed anteriorly to simplest posteriorly. QMF772 (Woods, 1958, fig. 1) also shows a lingual accessory midlink gradient, and is intermediate in development between the other two specimens. SAMP31370 and 31371 (Pledge, 1991, fig. 4) also show the lingual midlink. P186593 from the Wyandotte LF (McNamara, 1990) does not show the midlink at all, and it is unclear in the worn holotype BM46316 and AMF7272. The extreme expression of this char-



1. Riversleigh (α) 1
2. Wyandotte (α?) 2
3. Bluff Downs (σ) 1
4. Alcoota (ϖ) 5
5. Chinchilla Sands (β, χ) 3
6. Eastern Darling Downs - Macalister, Gowrie, Kings Creek, Warra, St. Ruth (α, χ, β) 11
7. Cement Mills, Gore (α, β) 2
8. Tea Tree Cave (χ) 1
9. Myall Creek (α) 1
10. Bow (β) 1
11. Cuddy Springs (χ) 1
12. Wellington Caves (α, β) 3
13. Wee Jasper Caves (β) 1
14. Grong Grong (α) 1
15. Buchan Caves (α, χ) 4
16. Gipp's Land, Tambo River (α) 1
17. Sorrento (α) 1
18. Werribee (α) 1
19. Hamilton Grange Burn (?ϖ) 1
20. near Keilor (α) 1
21. Terang (α) 1
22. Spring Creek (α) 1
23. Strathdownie (α, β) 2
24. Goulden's Hole Cave (β) 2
25. Henschke Fossil Cave (?α) 2
26. Victoria Cave (α) 1
27. Thebarton (α) 1
28. Toolapinna Fauna, Warburton River (?α) 1
29. Curramulka (α) 1
30. Scotchtown Cave (χ) 1
31. Mowbray Swamp (α) 1
32. Pulbeena Swamp (α) 1

uncertain locality (α, β, χ) 26 specimens

KEY TO SPECIES SYMBOLS

(α) *P. azaei, P.* cf. *azaei*
(β) *P parvus, P.* cf. *parvus*
(ϖ) *P. painei*
(σ) *P. selestiae*
(χ) *P.* sp., *P.* sp. nov, *P. sp.* indet.

FIG. 2. Distribution of *Palorchestes* in Australia. The minimum number of individuals at each site (number after the species symbol in the site listing) includes published and unpublished specimens.

acter in QMF30882 is within the intraspecific range of variation.

The large variation in molar size for *P. azaei* (Table 1), coupled with intraspecific variation support Woods' (1958) view that it is a highly variable species. Molar morphology grades along the tooth row from complex anterior molars with additional links to simple diprotodontid-like teeth posteriorly. Sample sizes are too small to estimate coefficients of variation for molar dimensions, or identify sexual dimorphism.

The Riversleigh specimen is larger than *P. parvus* from the early Pliocene Chinchilla Sand (Woods, 1958) (Table 1). Its molars are relatively broader resulting in squarer molars in occlusal view. The lack of a double hindlink on the M^1 as in QMF789 (Darling Downs;Woods, 1958, fig.4) and NMVP48987 (Buchan Caves) also distinguishes the two species.

The Riversleigh specimen differs from *P. selestiae*, from the early Pliocene Bluff Downs Local Fauna (Mackness, 1995), in being about 25% smaller and in the lingual forelink being in contact with the anterior cingulum rather than terminating in the cingular basin.

It differs from *P. painei*, from the late Miocene at Alcoota (Woodburne, 1967) in being significantly larger (Table 1), with more complex molar morphology including higher crowns, having a double forelink on M1, and in having a single midlink on M2.

DISCUSSION. Over 80 Plio-Pleistocene *Palorchestes* specimens have been registered with museums from at least 32 open sites and cave deposits throughout Australia (Fig.2). *P. azaei*, the most widely distributed species, is present in 21 of the 32 sites.

Few sites with *P. azaei* have radiocarbon dates available. Published dates range from

19,800±390 BP at Spring Creek (Flannery & Gott, 1984) to 54,200 +11,000 -4,500 BP at Pulbeena Swamp (Banks et al., 1976) and 30,400 +750 -700 BP at Wyandotte (McNamara, 1990). Specimens at Wellington Caves, Naracoorte Caves (Wells et al., 1984) and the Warburton River (Toolapinna Fauna; Tedford et al., 1992) could be considerably older.

The presence of 2 species of *Palorchestes* at Cement Mills (Bartholomai, 1977), Wellington Caves, Buchan Caves, and Strathdownie (Flannery & Archer, 1985) has been interpreted by some to mean that they are mixed Pliocene and Pleistocene assemblages. Alternatively *P. parvus* may have extended into the Pleistocene as suggested by Bartholomai (1977) or Pleistocene *P. parvus* may be incorrectly assigned.

Although widespread, *P. azael* specimens are rare at any one site, generally being represented by only one or two individuals and no other fossils (at least 8 known sites) or a single specimen of *P. azael* with associated faunas (at least 8 sites). The low density may be an artefact of preservation, but could indicate that *P. azael* was a solitary animal (Flannery & Archer, 1985).

At Terrace Site *P. azael* is associated with the large to medium-sized herbivores in a fauna dominated by riverine turtles, crocodiles, water rats and fish (Archer et al., 1994). The palaeoenvironment is interpreted to have been similar to that which characterises the area today (Archer et al., 1994). The other northern Queensland assemblage, the Wyandotte Local Fauna (McNamara, 1990), contains a similar faunal assemblage. More southern faunas are dominated by large browsing and grazing mammals (e.g. *Diprotodon optatum* and diverse *Macropus*, *Protemnodon* and *Sthenurus* spp.) in open sclerophyll forest (Bartholomai, 1977), *Eucalyptus* woodland (Banks et al., 1976), low heath (Flannery & Gott, 1984) and trees & shrubland (Dodson et al., 1993). *P. azael* evidently tolerated a wide range of climatic conditions and habitat types.

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